THE MORPHOLOGY OF THE PERIDIAL CELLS IN THE ROESTELIAE[1]

FRANK DUNN KERN

(WITH PLATES XXI AND XXII AND TWO FIGURES)

While making a study of the morphological characters of various species of Roestelia, attention has been especially attracted to the peridial cells. They are much more characteristic than are the roestelial spores, and so strikingly different, except in two known cases, from the peridial cells of the aecia of pucciniaceous species that they are at once conspicuous upon the most cursory examination. The two exceptions just cited are *Aecidium Blasdaleanum* D. & H. and *Aecidium Sorbi* Arth., which are classed with the Roesteliae on account of their life histories, but which have the morphological characters of the pucciniaceous aecia and are therefore not included in the discussions in this paper. The taxonomic importance of the peridial cells in defining the species of Roestelia has been ably pointed out by Dr. ED. FISCHER,[2] and a number of American species have been figured and described[3] in considerable detail by him. FISCHER took into account only the surface sculpturing on the cells, but aside from this there are a number of other features of the morphology which seem worthy of consideration. The microscopical structure is described with some detail in this paper, with the hope that it may be of interest.

The manner in which the individual cells are joined together to make up the peridium is one of the first characteristics worthy of mention. If a bit of the mature peridium of almost any of the species is mounted in water for a microscopical examination, the cells are usually seen separated from one another, or perhaps a few short chains made up of cells attached together at the ends remain. In case the cells do not separate while the mount is being prepared, a

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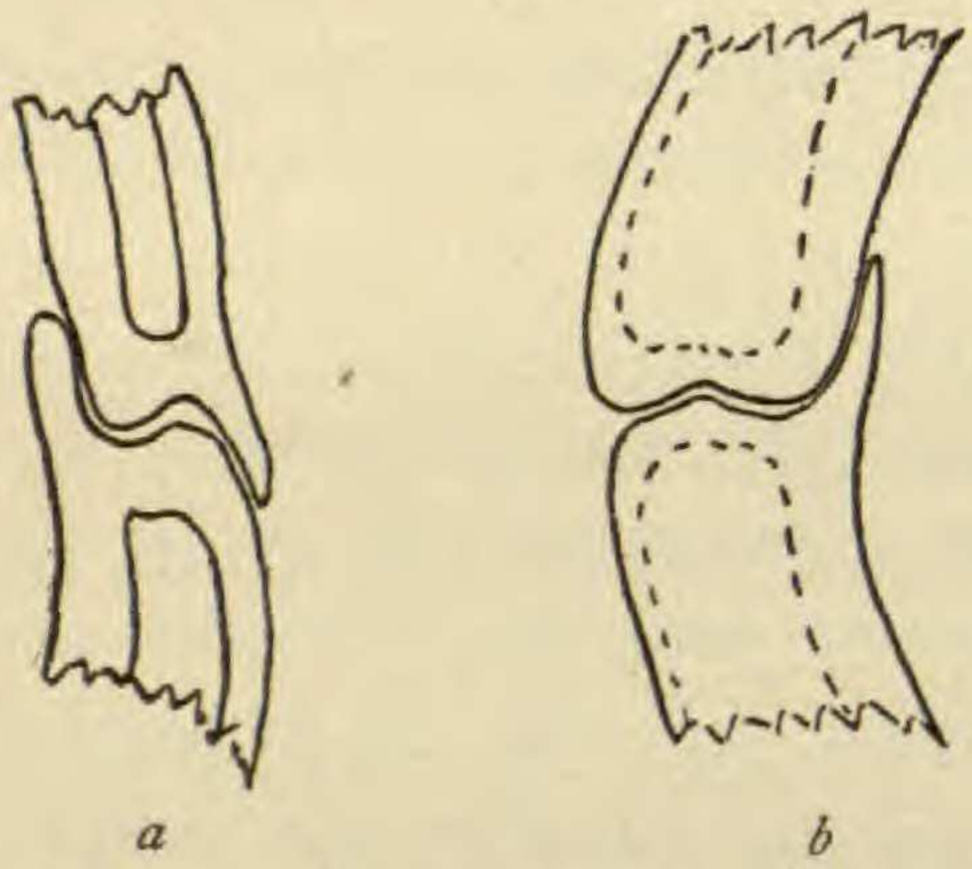
[2] Zeit. f. Pflanzenkr. **1**:271. 1891.

[3] Hedwigia **34**:3, 4. *figs. 1–10*. 1895.

slight movement of the cover glass will usually serve to dislodge them. This loose union along the sides of the cells as they are joined to make up the peridial tissue, tends to make the peridium rupture at its maturity by longitudinal slits along the sides rather than at the apex, and gives the lacerated and fimbriated appearance so characteristic of most of the species. Only two species of the true Roestelia type have been observed which have peridia that do not become more or less split up; these are *R. Harknessiana* E. & E., an unattached species from California, and *G. inconspicuum* Kern (*R. Harknessianoides* Kern), from the western mountain region. In these the peridia are firm and remain tubular even after months of weathering.



a *b*

FIG. 1.—Showing how the cells of some species are joined end to end; the portions uppermost are toward the apex of the peridium; in *a* the outer wall of the upper cell overlaps considerably; in *b* this is much less pronounced.

The way in which the cells are joined end to end is another distinctive feature of this group. In addition to being imbricate, a character common to many aecial forms, the ends of the cells are, with a few possible exceptions, articulated in such a manner as to make movable joints (*text fig. 1*). This power of yielding at these joints permits the ruptured peridium to curl and twist in a manner particularly prominent in some of the species.

In shape one finds a considerable variety. In some species the cells are long and thin (*figs. 7, 12*), in others short and very stout (*figs. 8, 15, 16*). With respect to shape, it is necessary to consider the cells from two points of view, viz., side view and face view. The side view, which is the longitudinal radial view, shows the dimensions of length and thickness. In this view the outer and inner walls are practically parallel. In some of the species which have short and rather thick cells, the imbrication at the ends gives an oblique effect which makes a rhomboidal shape (*figs. 15, 16*). Where they are longer and thinner, the length becomes more pronounced, and linear-

rhomboidal (*figs. 3, 4, 10*) is a more accurate description; or where the length is very great comparatively, the obliqueness at the ends is inconspicuous and they may best be described as linear (*fig. 7*). In face view, which is the longitudinal tangential view, length and breadth are the dimensions in the plane of vision. The cell may be regarded as having two faces, the one which is to the outside, and the one which is to the inside as it is in place in the peridial wall. The distance from the outer face to the inner face constitutes the thickness of the cell. In considering shape in face view it makes no difference which face is turned toward us. The cells of some of the species are not easily seen in face view, but of those that will lie so as to be readily examined the majority do not have the side walls parallel, but vary from lanceolate or broadly lanceolate (*fig. 16*) to polygonal-ovate or polygonal-oblong (*fig. 9b*). Most of the cells are more or less narrowed both above and below (*fig. 17b*). There is one species, *G. Botryapites* (Schw.) Kern (*R. Ellisii* Peck), which does not conform to any of the shapes mentioned. It has cylindrical hypha-like cells which are sometimes irregularly bent (*fig. 12*).

The accompanying table will serve to show the variation in size of the cells and in thickness of the walls. In the measurements given an attempt is made to make some allowance for the variation within any particular species, it being the case in most instances that the cells near the apex are proportionately shorter. *G. Bermudianum* (Farl.) Earle, the only autoecious species known to exist, has the shortest cells of any examined (*fig. 1*). The maximum length is three to four times greater than the minimum, and is found in the cells of *R. transformans* Ellis (*fig. 7*), a species developing in the leaves and fruit of *Aronia arbutifolia* (*Pyrus arbutifolia*). In most of the species the breadth is greater than the thickness, but in three or four (nos. 9, 14, 15, 16 in the table) having especially firm peridia, which do not become much split or lacerated, the reverse is the case.

With respect to thickness of walls, the general type of peridial cell has inner and side walls rather thick with outer wall rather thin. The side walls appear to be about equal in thickness with the inner wall in the species where the inner wall is only moderately thickened (*text fig. 2, a, b*). In some very thick and proportionally narrow cells, where the inner wall is excessively thickened, the side walls

are much less and become gradually thinner toward the outer side of the cell (*text fig. 2c*). The outer wall is usually never more than half as thick as the inner and is commonly considerably less. There are two exceptions to the above statements which should be noted here, *G. Botryapites* (Schw.) Kern (no. 12), which has the conditions of

TABLE SHOWING SIZE AND THICKNESS OF WALLS OF PERIDIAL CELLS IN SIXTEEN SPECIES OF ROESTELIA*

SPECIES †	LENGTH (FROM END TO END)	BREADTH (FROM SIDE TO SIDE)	THICKNESS (FROM FACE TO FACE)	THICKNESS OF WALLS	
				Outer wall	Inner and side walls
1. G. Bermudianum	50–75 μ	18–25 μ	15–18 μ	1.5 μ	3–5 μ
2. G. Juniperi-virginianae (*R. pyrata*)	65–100	(16–22)	10–16	2.5–3	4–6
3. G. floriforme	65–85	(14–18)	10–14	1.5–2	4–5
4. G. globosum	60–90	15–23	13.19	1.5	3–5
5. G. Betheli	60–90	20–25	13–20	1–1.5	4–6
6. G. clavariaeforme (*R. lacerata*)	80–130	18–30	15–25	1–2	5–7
7. R. transformans	150–300	(20–30)	12–18	2–3	4–6
8. G. juniperinum (*R. penicillata*)	60–90	(45–55)	30–35	2–3	7–10
9. G. germinale (*R. aurantiaca*)	45–95	19–39	25–40	3–5	13–23
10. G. Nidus-avis (*R. Nidus-avis*)	55–88	15–23	14–18	1–1.5	5–7
11. R. hyalina	87–105	19–29	(20–26)	(12–16)	3–4
12. G. Botryapites (*R. Ellisii*)	145–190	9–14	9–14	1.5–2	1.5–2
13. G. Nelsoni (*R. Nelsoni*)	65–110	18–32	17–27	1–1.5	5·7
14. R. cornuta	60–110	19–29	30–35	2	8–12
15. G. inconspicuum (*R. Harknessianoides*)	65–100	25–35	45–55	5–8	20–35
16. R. Harknessiana	90–112	40–65	58–74	4–6	15–20

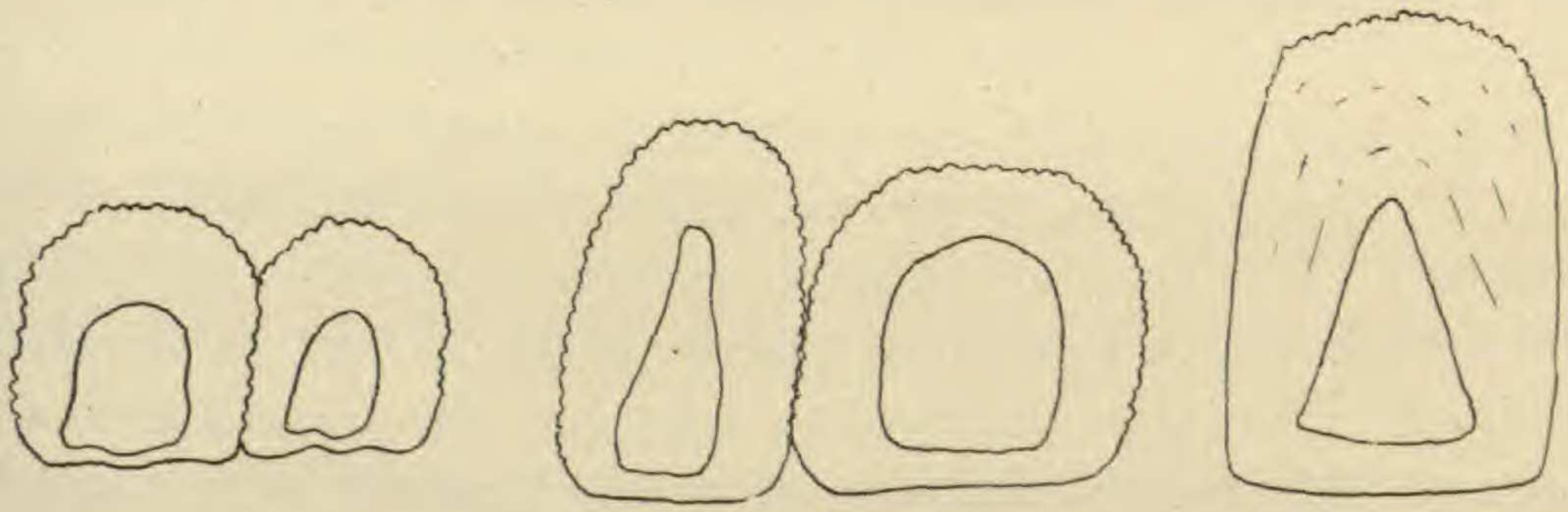
*Where the measurements are included within parentheses, it indicates that the cell, owing to some peculiarity in shape or to its hygroscopic properties, does not ordinarily lie in a loose water mount so that this measurement can readily be taken.

†Where the telial connection is known, the species are referred to Gymnosporangium in this table, with the roestelial name, if one exists, included as a synonym.

the general type reversed, a very thick outer wall and rather thin inner wall (*fig. 11a*). The table indicates the variations to be found in a number of species. Not taking into account the exceptions noted above, the thinnest outer wall found was 1 μ, while the thickest was 8 μ. The inner and side walls vary from 3 or 4 μ (*figs. 1, 4*) to 35 μ (*fig. 16*).

The cells of some of the species when examined in loose mounts may be seen easily in either face or side views. When this is the

case the cells lie straight, and there is usually not much disparity between the breadth and thickness (*figs. 1, 10, 13, 14*). There are a number of species, however, in which the cells tend to lie only on their sides when mounted in water, and it is only with difficulty that a face view can be observed. The cause for the cells taking this position is that they become much curved in water (*figs. 2, 5, 6, 7*), and their equilibrium, therefore, is much more stable when they lie on their sides. Such cells are hygroscopic and will straighten out when they become dry. It has been found that the curvature



a *b* *c*

FIG. 2.—Cross-sections of peridial cells of several species: inner walls are above in the drawings; *a*, *G. clavariaeforme* (redrawn from FISCHER), inner and side walls of almost equal thickness; *b*, *R. cornutum*, inner and side walls of about same thickness; *c*, *G. inconspicuum*, inner wall excessively thickened, side walls not so thick, becoming thinner toward outside.

is always inward, the outer wall being on the outer side of the curve. It is interesting to note the effect which this incurving of the individual cells has upon the peridium as a whole. *R. pyrata* (Schw.) Thaxt., the aecial stage of *G. Juniperi-virginianae* Schw., is one of the species which has very marked hygroscopic cells. In the ordinary dried condition of herbarium specimens, the peridium of this species is finely fimbriate and strongly recurved, giving the appearance of having been combed outward. In a saturated atmosphere or in any way under the influence of moisture, the revolute chains of cells may be seen to unroll themselves and take a more or less erect position, or even become somewhat bent inward. They assume their recurved position again upon drying.

With regard to the surfaces of the peridial cells, it has been found that the species so far recognized divide at first into two classes, one

having entirely smooth cells, the other having at least a portion of the surface roughened. I have subdivided the latter class upon the nature of the roughness, and have used the terms rugose, verrucose, verruculose, and spinulose to designate the four subdivisions.

Very little comment is needed for the class having smooth cells. It is the exception to the general rule, only two species being known which belong here. One is *R. hyalina* (*fig. 11*) and the other is *G. Botryapites* (*fig. 12*). These are unusual forms in other ways, as seen by the fact that both have been mentioned previously as being the only forms not conforming to the general type with respect to thickness of walls. Thus it will be seen that nearly all of the species have peridial cells which are sculptured in some way. No single word or even a single phrase will suffice for a description of the markings. It is necessary in most instances to resort to rather long and complicated sentences to convey details enough to be fairly accurate. The terms employed to designate the various classes are intended only to be descriptive in a general way. The rugosely sculptured cells are furnished chiefly with ridges or with elongated ridgelike papillae in such a way that the effect is that of a surface covered with rugae or folds; the verrucosely marked cells are studded with warty or tubercle-like elevations; the verruculose surfaces are covered with low wartlike protuberances; the spinulose cells have diminutive spines or spicules.

The markings always cover the entire inner wall (*figs. 1b, 9b, 17b*), extending to the side walls, in some forms reaching clear across (*figs. 1a, 3, 4, 8, 10, 13, 14, 16*), in others only a part of the distance (*figs. 2, 6, 7, 9a, 15*), leaving the remaining outer part of the side wall and the entire outer wall, with one exception, smooth. Only one species has been found which is an exception to this general type; it differs in having the outer wall also sculptured. This is an undescribed and unattached species (not included in the table), and is further notable in being the only one having cells with spinulose warts (*fig. 17*).

Of the sixteen species enumerated in the table, one-half have rugosely sculptured cells, nos. 1, 2, 3, 4, 5, 8, 10, 14.[4] In all these the ridges or ridgelike markings begin on the inner wall (as in *fig. 1b*),

[4] These numbers also correspond to the figure numbers on the plates.

and are directed downward and outward and extend obliquely on to the side walls. In some species the ridges are of uniform width (*figs. 5, 10, 14*), in others they become somewhat broader toward the outer side (*fig. 2*). In some species the long ridgelike markings are closely and rather evenly arranged (*figs. 3, 10*), while in some they are rather sparsely set with separate and shorter, sometimes roundish papillae in the intervening spaces (*figs. 2, 5, 8*). Nos. 6, 7, 9, 15, and 16[5] have verrucosely roughened cells. The warts vary from roundish or slightly irregular (*figs. 6, 7, 15, 16*) to very irregularly branched forms (*fig. 9*), and are arranged without apparent order. They are usually more sparse toward the outer portion of the side walls. The verrucose character is pronounced in only one form, *G. Nelsoni* Arth., which consequently occupies this class by itself (*fig. 13*).

PURDUE UNIVERSITY
LAFAYETTE, INDIANA

EXPLANATION OF PLATES XXI AND XXII

The drawings were outlined with the aid of a camera lucida at a uniform magnification of 625 diameters, and were reduced about one-fifth in reproduction. In every case the end which is uppermost on the plate is the upper end of the cell, or, in other words, the end which is toward the apex of the peridium. In all figures except *11* and *12* the inner wall can readily be distinguished by its relatively greater thickness.

PLATE XXI

FIG. 1.—*G. Bermudianum* Farl.: *a*, side view; *b*, face view.
FIG. 2.—*G. Juniperi-virginianae* Schw. (*R. pyrata* [Schw.] Thaxt.).
FIG. 3.—*G. floriforme* Thaxt.
FIG. 4.—*G. globosum* Farl.
FIG. 5.—*G. Betheli* Kern.
FIG. 6.—*G. clavariaeforme* (Jacq.) DC.
FIG. 7.—*R. transformans* Ellis.
FIG. 8.—*G. juniperinum* L. (*R. pennicillata* [Pers.] Fries.).
FIG. 9.—*G. germinale* (Schw.) Kern (*R. aurantiaca* Peck).

PLATE XXII

FIG. 10.—*G. nidus-avis* Thaxt.
FIG. 11.—*R. hyalina* Cooke: *a*, side view, the thick wall is the outer wall here; *b*, face view.

[5] These numbers also correspond to the figure numbers on the plates.

FIG. 12.—*G. Botryapites* (Schw.) Kern (*R. Ellisii* Peck): the inner wall is the one to the right.

FIG. 13.—*G. Nelsoni* Arth.

FIG. 14.—*R. cornuta* (Pers.) Fries.

FIG. 15.—*G. inconspicuum* Kern (*R. Harknessianoides* Kern).

FIG. 16.—*R. Harknessiana* Ellis & Ev.

FIG. 17.—*Roestelia* sp., an unnamed species, the only one having spinulose markings: *a*, side view; *b*, face view.